

SEASONAL ACTIVITY AREAS OF COYOTES IN THE BEAR RIVER MOUNTAINS OF UTAH AND IDAHO

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Abstract: We studied the seasonal movement patterns and dispersal of coyotes (*Canis latrans*) in the Bear River Mountains of northern Utah and southern Idaho to determine whether coyotes in this montane region exhibit an altitudinal migration on a seasonal basis. We used 3 locational parameters to assess whether a seasonal altitudinal migration was evident, including overlap in seasonal activity areas, distance between harmonic mean centers of activity, and seasonal differences in mean elevations of locations. Winter and summer activity areas of every mature coyote overlapped, with mean distances between harmonic centers of seasonal activity of 1.5 km (range = 0.4–3.3 km). Conversely, there was no overlap between summer and winter activity areas of any subadult coyotes, with mean distances between their harmonic seasonal centers of activity of 35.8 km (range = 16.7–68.4 km). Significant changes in elevation of seasonal locations were not evident for any sex or age group. We conclude that the movement of subadult coyotes in the Bear River Range was part of typical dispersal behavior and was not motivated by seasonal change, with such wandering generally ceasing during the coyotes' second year of age. We also conclude that adult coyotes utilized similar areas in summer as in winter, with no evidence of seasonal movements between mountain and locations at lower elevations.

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Most previous studies of coyote activities in montane environments have primarily involved valley and riparian areas (Bowen 1982, Gese et al. 1996, Arjo and Pletscher 1999, 2004). Robinson and Cummings (1951) conducted an extensive tagging study in Yellowstone National Park, but the majority of their efforts also were directed primarily at riverine or valley populations. Exceptions to this generalization include Hawthorne (1970) and Shivik et al. (1997), who studied coyotes in the Sagehen Creek Basin of the Sierra Nevada. Based on observations in the intermountain area indicating coyotes are frequently found near concentrations of big game animals in winter (e.g., Nielsen 1975), conventional wisdom suggests coyotes in such areas migrate on a seasonal basis to lower elevations where food resources may be more accessible during winter (Nielsen 1975). On the other hand, coyotes are typically territorial year-round (Camenzind 1978, Windberg and Knowlton 1988, Gese et al. 1996, Arjo and Pletcher 1999, Knowlton et al. 1999, Blejwas 2002) and would be expected to defend those territories during courtship, breeding, and pup-rearing. Since pair-bonding among coyotes begins in late fall, continues through winter, with breeding occurring in late January

through February, biological constructs suggest they should defend territories in montane habitats even in rigorous winter conditions.

Inherent in addressing the issue of presence or absence of an altitudinal migration among coyotes in montane habitats is discrimination between migration and dispersal. Migration would anticipate a cyclic change in primary areas of activity, presumably on a seasonal basis. Dispersal, on the other hand, should involve individuals leaving 1 area of activity with an apparent intent of establishing another area of activity and not involve an attempt to reoccupy the former area. Dispersal is typically associated with, but not limited to, younger age classes (Davison 1980, Bowen 1982, Andelt 1985).

Interpretations take on added significance from the perspective that some coyotes are found at high elevations during winter near areas used by domestic sheep in summer. Sheep using these mountain grazing allotments are frequently preyed upon by coyotes (Klebenow and McAdoo 1976, Nass 1977, Taylor 1977, Tigner and Larson 1977, Wagner 1988, Wagner and Conover 1997). Efforts to curtail such depredations frequently rely on aerial gunning to remove coyotes from these allotments during winter when habitat and flying conditions make such activities safer and more effective. Detractors of such actions suggest coyote movements, as well as the 4- to 6-month interval between coyote removal and the presence of

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sheep, make it unlikely the appropriate coyotes are removed.

To explore biological aspects involved in this controversy, we used 3 parameters based on radio telemetry locations to assess whether or not coyotes inhabiting mountainous areas of northern Utah and southern Idaho are involved in altitudinal migrations on a seasonal basis, including overlap in seasonal telemetry locations, distances between harmonic mean seasonal centers of activities, and differences in elevation of seasonal locations.

STUDY AREA

Our study site consisted of 2,176 km² of the Bear River Mountains straddling the Utah-Idaho border. It comprised portions of the Caribou and Wasatch-Cache National Forests and included some state and private lands. The topography is steep mountains, deep narrow canyons, and high mountain valleys and flats with elevations ranging from 1,425 m at the mouth of Logan Canyon to 3,042 m on Naomi peak. The climate was representative of semi-arid, high-desert mountains. The average, annual precipitation was 86 cm, the majority of which occurred as snow. Annual snowfall averaged 756 cm (Brough et al. 1987) with the first permanent snowfall usually occurring in November and the ground remaining snow-covered until May or June (Schimpf et al. 1980, Brough et al. 1987). Average monthly temperatures ranged from a maximum of 24°C in July to a minimum of -15°C in January (Brough et al. 1987).

The predominant vegetation varied from grassland-shrub communities on flat areas and southern exposures to coniferous forests at high elevations and northern exposures. Stands of aspen (*Populus tremuloides*), subalpine fir (*Abies lasiocarpa*), Douglas fir (*Pseudotsuga menziesii*), limber pine (*Pinus flexilis*), lodgepole pine (*Pinus contorta*), and big-toothed maple (*Acer grandidentatum*) were common. Shrub species included mountain mahogany (*Cercocarpus ledifolius*) and big sagebrush (*Artemisia tridentata*), and common graminoids were bluebunch wheatgrass (*Agropyron spicatum*), slender wheatgrass (*A. trachycaulum*), Idaho fescue (*Festuca idahoensis*), and mountain brome (*Bromus carinatus*). Nomenclature of vegetation follows Welch et al. (1987).

Mammalian co-inhabitants of the area included elk (*Cervus elaphus*), moose (*Alces alces*), mule deer (*Odocoileus hemionus*), badger (*Taxidea taxus*), striped skunk (*Mephitis mephitis*), snowshoe hare (*Lepus americanus*), porcupine (*Erethizon dorsatum*),

red squirrel (*Tamiasciurus hudsonicus*), and various other rodents. While most ungulate species were found throughout the study area in summer, most moved to locations below 2,000 m in winter (Carpenter and Wallmo 1981, Wallmo and Regelin 1981).

METHODS

Coyote Capture and Handling

We conducted coyote capture efforts from 1 to 25 September 1987 and 14 August to 3 October 1988. The rugged nature of portions of the study area limited our trapping efforts to small areas (15–30 km of unimproved roads and trails) at any 1 time. To capture coyotes, we used Number 3 Victor foot-hold traps (Animal Trap Company, Letitz, Pennsylvania, USA) to which we attached tranquilizer trap devices (Balser 1965, Linhart et al. 1981, Sahr and Knowlton 2000) containing 600 mg of propiopromazine hydrochloride to reduce capture injury and distress. We darted 1 animal from a helicopter (Baer et al. 1978) using a mixture of ketamine hydrochloride (100 mg) and acepromazine (1.0 mg). We used the same mixture to sedate animals for transport and handling. We took coyotes to the National Wildlife Research Center field station near Millville, Utah, or to a camp within the study area for handling and observation during recovery from the tranquilizer. We tagged coyotes in each ear with uniquely numbered metal tags, fitted them with 164-MHz radiotelemetry collars (Telonics, Inc., Mesa, Arizona, USA), extracted a premolar for age determination via counts of cementum annuli (Linhart and Knowlton 1967), as well recorded data on capture date, location, and sex. We typically held coyotes overnight and released them at their respective capture sites the following day.

Data Collection

We determined locations of radiocollared coyotes from fixed-wing aircraft, as described by Mech (1983), Knowlton (1995), and Gantz (1990) between 13 November 1987 and 15 September 1989. L. C. Stoddart (National Wildlife Research Center, personal communication) and G. F. Gantz (Utah State University, personal communication) calculated a mean operational error of the aerial telemetry locations at 101 m (SE = 17 m) during a formal accuracy test in this topography. However, informal assessments made outside the test situation suggested locational errors during routine operations may have been twice as great. We de-

terminated daylight locations (typically morning) for each animal 1 to 10 times per month (0–2 per week), with greater emphasis on the summer grazing and winter aerial gunning periods. We identified aerial telemetry locations by visual reference to topographic features and recorded them on 1:24,000-scale U.S. Geological Survey topographic maps (Carrel et al. 1997) along with the date, time, and status (alive or dead) based upon motion-sensing circuitry in the transmitter.

Data Analysis

We identified radiotelemetry locations within 2 primary seasons of interest. Winter (1 Dec–31 Mar) coincided with the aerial-gunning season and the presence of continued snow pack, and summer (15 Jun–15 Sep) corresponded with the sheep grazing period.

We partitioned the location data for radiocollared coyotes by sex and age and assumed 15 April to be the date of birth for all coyotes on the study area. Data collection was clustered during winter and summer periods to enhance interseasonal comparisons among the following age classes: juveniles in winter and yearlings in summer (9–18.5 months), yearlings in summer and the following winter (15.5–24.5 months), yearlings in winter and adults in summer (21–30.5 months), and adults between summer and winter (≥ 27.5 months).

We assigned universal transverse mercator (UTM) coordinates and elevation for each location. We calculated the seasonal activity areas and harmonic mean centers of activity for each radiocollared coyote with program HOME RANGE (Samuel et al. 1985a), which uses an extension of the harmonic mean measure of activity (Dixon and Chapman 1980). HOME RANGE determines a utilization distribution by estimating the probability of use at any location in the activity area (Samuel et al. 1985a). Harmonic mean centers of activity indicate the true centers of activity (Dixon and Chapman 1980). Some locations were identified as outliers by program HOME RANGE based on having bivariate normal weights < 0.6 (i.e., distances to the other locations were great). Since outliers disproportionately affect estimates of activity area size, we excluded them from the analyses and from subsequent calculations (Samuel and Carlton 1985; Samuel et al. 1985a,b). We then defined activity areas by the area encompassed by the 85% harmonic utilization contour, excluding those comprised of < 10 locations from the analysis to reduce errors associated with small sample sizes (Samuel et al. 1985a).

We used coyotes for which we determined activity areas in consecutive seasons to determine whether coyotes may have migrated on a seasonal basis. We combined plots from adjoining seasons for each animal and examined them visually to determine whether activity area contours overlapped. When displayed graphically, the pattern of distances between seasonal harmonic mean centers of activity as a function of animal age were sufficiently distinct to preclude the need for inferential statistics (Cherry 1998, Johnson 1999). We also visually examined changes in mean elevations of locations for each animal on a seasonal basis.

RESULTS

Characteristics of the Data

We captured 21 coyotes, 2 juveniles (1M, 1F) and 1 adult (M) in 1987, and 8 juveniles (4M, 4F), 8 yearlings (4M, 4F), and 2 adults (1M, 1F) in 1988 (Table 1). We monitored individual radiocollared coyotes for zero to 23.7 months ($\bar{x} = 8.9$, $SD = 5.9$); 10 of which died before completion of the study, and 4 moved off the study area. Three of these moved to sites physiographically similar to the study area, while a fourth moved into farmland but returned 2 weeks later.

Area of Use

We used data from 16 coyotes (8M, 8F) with ≥ 10 locations within at least 1 season to assess relative size of their seasonal activity areas (Table 1). The numbers of locations used to determine seasonal activity areas for individual coyotes ranged from 10 to 28 ($\bar{x} = 18.5$, $SD = 3.23$, $n = 30$), with ≤ 3 ($\bar{x} = 0.80$, $SD = 1.00$, $n = 29$) outliers identified by program HOME RANGE.

The mean size of activity areas decreased nearly 7-fold with age, from 71 km² among juveniles during their first winter, to 10 km² among adult coyotes (Fig. 1). Activity areas of coyotes < 19 months old were larger than coyotes ≥ 19 months old (Fig. 1). Variance in mean size of activity areas also decreased with coyote age (Fig. 1).

We used data from 11 coyotes (5M, 6F) to assess inter-seasonal movement patterns (Table 2). Information from 2 coyotes spanned 4 and 3 seasons, respectively, permitting 5 interseasonal comparisons between them. Twelve of 14 interseasonal activity area comparisons were winter to summer. The 3 parameters we used to assess interseasonal movement patterns were: (1) seasonal overlap in activity areas, (2) distance between harmonic centers of activity, and (3) changes in mean elevation. One

Table 1. Age, sex, tenure in study, and number of radiolocations obtained on coyotes in the Bear River Mountains, Utah, USA, 1987–1989.

Animal no.	Sex	Age ^a	Tenure in study (mo.)	No. of radiotelemetry locations			
				1987–1988		1988–1989	
				Winter	Summer	Winter	Summer
1	M	Juvenile	4.7	20			
2	M	Juvenile	7.0			16	
3	M	Juvenile	12.6			18	16
4	F	Juvenile	11.6			16	19
5	F	Juvenile	11.9			17	21
6	F	Juvenile	17.5		19	17	21
7	F	Juvenile	23.7	28	19	19	21
8	M	Yearling	11.5			16	21
9	M	Yearling	11.9			17	21
10	M	Yearling	13.0		5	19	21
11	F	Yearling	4.3			10	
12	F	Yearling	7.6			16	2
13	F	Yearling	11.8			16	20
14	M	Adult	4.1	13			
15	M	Adult	11.4			17	22
16	F	Adult	11.6			17	21

^a Age at capture (juvenile = 12 mo., yearling = 12–23 mo., and adults = >24 mo.).

coyote traversed a very large area during the summer of 1989 and was excluded from this analysis.

Activity areas from adjacent seasons for individual coyotes overlapped in 64% of the comparisons. One of 2 yearling–yearling, all yearling–adult, and all adult–adult comparisons had overlapping activity areas between seasons. None of the juvenile–yearling comparisons nor the other yearling–yearling comparison had overlapping activity areas in adjacent seasons (Table 2).

Mean distances between harmonic centers of activity for inter-seasonal comparisons among age classes ranged from 0.4 km (yearling–adult) to 68.4 km (juvenile–yearling; Table 2). The difference in the mean distance between seasonal centers of activity of coyotes <19 months old (juvenile–yearling) and those ≥19 months old (yearling–adult and

adults) is evident (Fig. 2). Mean distances between seasonal centers of activity for coyotes <19 months old (\bar{x} = 35.8 km, SE = 11.3, n = 4) was 24 times larger than the mean for coyotes ≥19 months old (\bar{x} = 1.5 km, SE = 0.3, n = 8). There also was greater variation in distances between seasonal centers of activity for younger coyotes than older ones (Fig. 2).

Inter-seasonal changes in the mean elevations of locations for individual coyotes ranged from –500 m (juvenile–yearling) to +400 m (yearling–yearling; Fig. 3). Although differences were not large, mean elevations of locations for 9 of 14 coyotes appeared slightly higher in winter than in summer. No relationship between change in elevation and age or sex was evident.

Dispersal Patterns

Coyotes that moved long distances traveled primarily north and south, paralleling the axis of the Bear River Range, rather than east–west. The latter could have moved them into valleys on either side of the range. The harmonic center of activity for 4 coyotes shifted 11.8, 16.7, 27.8, and 68.4 km south, respectively, while 1 coyote shifted 30.4 km north. The maximum separation of locations for 2 coyotes were 81.8 and 129.5 km in 150 and 44 days, respectively, in north–south directions.

DISCUSSION

Characteristics of Activity Areas

We did not acquire sufficient telemetry locations to describe home-range characteristics in any con-

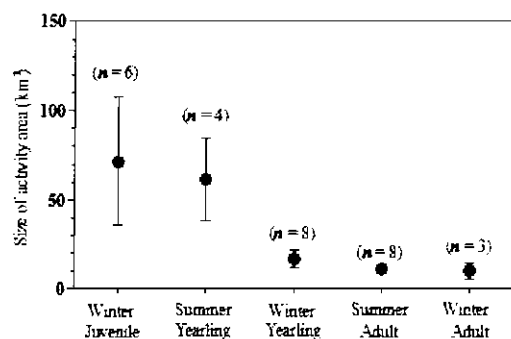


Fig. 1. Comparison of mean sizes (km²) of seasonal activity areas by age class of radiocollared coyotes in the Bear River Mountains, Utah and Idaho, USA, 1987–1988 (samples sizes and SE are indicated).

Table 2. Comparisons of interseasonal activity areas of coyotes, by age class, in the Bear River Mountains of Utah and Idaho, USA, 1987–1989.

Animal no.	Sex	Age	Season ^a	Overlap in seasonal ranges ^b	Distance (km) between centers of activity ^c
3	M	Juvenile-yearling	Winter–summer	No	68.4
4	F	Juvenile-yearling	Winter–summer	No	30.4
5	F	Juvenile-yearling	Winter–summer	No	27.8
7	F	Juvenile-yearling	Winter–summer	No	16.7
6	F	Yearling-yearling	Summer–winter	No	11.8
7	F	Yearling-yearling	Summer–winter	Yes	2.3
7	F	Yearling–adult	Winter–summer	Yes	2.1
8	M	Yearling–adult	Winter–summer	Yes	1.7
6	F	Yearling–adult	Winter–summer	Yes	1.6
9	M	Yearling–adult	Winter–summer	Yes	1.2
13	F	Yearling–adult	Winter–summer	Yes	0.6
10	M	Yearling–adult	Winter–summer	Yes	0.4
15	M	Adult–adult	Winter–summer	Yes	3.3
16	F	Adult–adult	Winter–summer	Yes	0.9

^a Winter = 1 Dec through 30 Mar; summer = 15 Jun through 15 Sep.
^b Based on 85% utilization contour from program HOME RANGE (Samuel, et al. 1985a).
^c Based on harmonic mean from program HOME RANGE (Samuel, et al. 1985a).

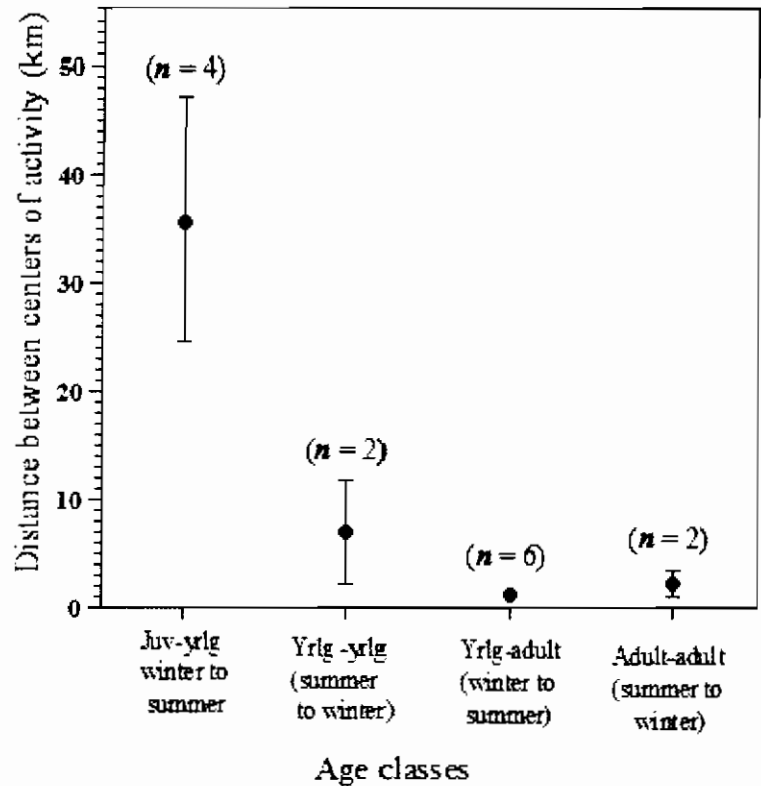


Fig. 2. Mean distance between seasonal harmonic mean centers of activity (km) by age class for radiocollared coyotes in the Bear River Mountains, Utah and Idaho, USA, 1987–1988 (sample sizes and SE are indicated).

ventional sense. However, we could readily categorize the coyotes we monitored into 1 group that had relatively large activity areas and another with much smaller activity areas. Similarly, we also could readily discriminate between coyotes that made appreciable changes in areas of activity from 1 season to the next and those that did not. With 1 exception, the 2 processes segregated the coyotes into groups that were identical and consistent with the relative ages of the animals. Activity areas for coyotes 8 to 17 months old were appreciably larger than those >19 months old. In addition, in the year following being radiocollared all coyotes <6 months old at the time also exhibited a significant change in centers of activity (\bar{x} displacements = 35 km), while the changes in mean centers of activity we observed among older coyotes was only 1.5 km. Furthermore, we are not aware of any of our juvenile coyotes returned to an original activity area. We consider the changes in activity areas among younger coyotes to be dispersal activities and unrelated to migration. This interpretation is consistent with the timing of major dispersal activities of coyotes described by others (Davison 1980, Bekoff and Wells 1982, Bowen 1982, Pyrah 1984, and Andelt 1985).

We interpret the data indicating summer and winter activity areas of coyotes in our study overlapped and the relatively short change noted in the mean change of summer and winter activity areas to infer that adult coyotes in this area do not migrate on a seasonal basis. This is supported by only slight changes in the mean elevations where the animals were located on a seasonal basis. If anything, elevations of estimated for winter locations were slightly higher than those calculated for summer locations. We conclude that adult, territorial coyotes in this area do not exhibit an altitudinal migration but maintain the same territories year-round. This is consistent with other research indicating coyotes maintain the same territories throughout the year (Camenzind 1978, Bowen 1981, Andelt 1985, Shivik 1995, Gese et al. 1996, Shivik et al. 1997) as well as with Weaver's (1979) suggestion that coyotes live in summer where they can survive in winter.

Dispersal Patterns

All dispersal type movements we observed paralleled the axis of the Bear River Mountains. If these coyotes had moved similar distances perpendicular to the axis of the mountains, many would have moved to valley locations at much lower elevations and presumably less rigorous environmental conditions. Only 1 coyote left the mountains, and that was for only a 2-week period in summer when it was located in foothill farmlands. Dispersing coyotes that traveled long distances did not leave montane habitats nor high elevations during winter. It appears that coyotes inhabiting mountains may be somewhat distinct from coyotes living in nearby valleys. This appears consistent with tagging studies of Robinson and Cummings (1951) where most coyotes tagged in valley locations were recovered in valley locations even though some moved considerable distances. Our observations are also consistent with that of

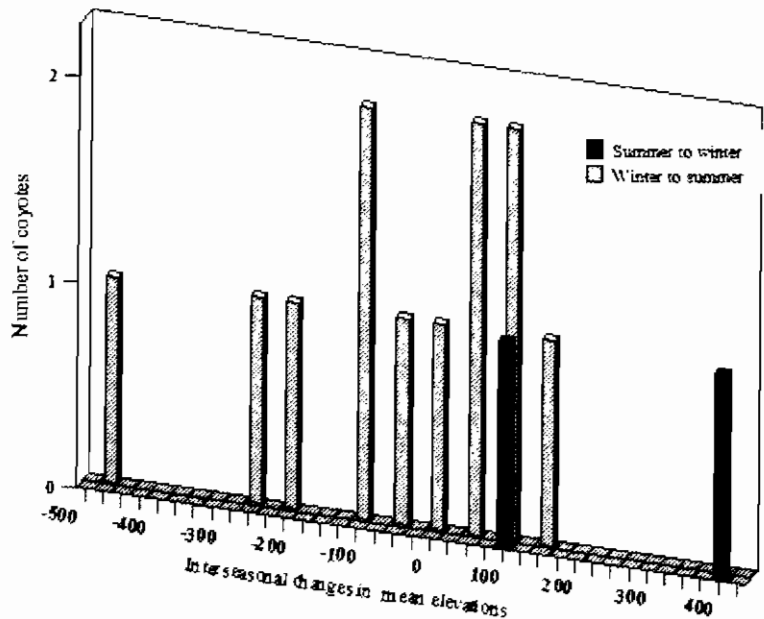


Fig. 3. Change in mean elevation (m), in 50-m increments, between summer and winter locations of radiocollared coyotes in the Bear River Mountains, Utah and Idaho, USA, 1987–1989.

Sacks et al. (2004, 2005) who used molecular genetic analyses to suggest genetic distances of coyotes are greater between adjacent bioregions than within bioregions. If correct, this may imply that coyotes imprint on natal habitat or topographic characteristics and seek similar areas when trying to establish territories of their own.

Knowing that many coyotes stay at high elevations during rigorous winter conditions increases our curiosity about how they subsist. Shivik et al. (1997) indicated coyotes in such situations reduce total activity, possibly to conserve energy. On the other hand, Weaver (1979) suggested the summer distribution of coyotes within Jackson Hole (Wyoming) reflected the winter distribution of ungulates, and presumably ungulate carrion. On several occasions we noted coyotes digging through 2–3 m of packed snow to retrieve parts of deer carcasses at a time when deer were not in the vicinity. Carcasses of unretrieved deer from the hunting season may permit coyotes to survive such rigorous conditions and occupy a niche that might otherwise be uninhabitable. This is consistent with observations of Todd and Keith (1976) and Weaver (1979) suggesting availability of winter carrion can be a major factor in maintaining coyote populations in the more harsh climates typical of northern portions of coyote distribution.

Our interpretations are subject to the cautions associated with small sample sizes in terms of the number of radiocollared coyotes involved and the number of radio locations used to assess characteristics of their activity areas. We believe, however, the nature of the data is sufficiently compelling to warrant consideration in management programs as well as future research designs pending development of more definitive information.

MANAGEMENT IMPLICATIONS

Current coyote management programs in mountainous areas of the west revolve primarily around reducing depredations on the domestic stock that use such grazing allotments in summer. This frequently entails removing coyotes via aerial gunning, typically in winter when foliage is less dense and high altitude flying conditions more safe. Other research indicates alpha coyotes in territorial social groups cause most depredations on sheep (Sacks et al. 1999, Blejwas 2002), especially those nurturing pups (Till and Knowlton 1983, Bromley and Gese 2001). Our data suggest coyotes removed from mountain pastures in winter include the territorial coyotes apt to be present the following summer. The later in the winter period coyotes are removed, the less likely territories will be re-populated by other territorial, and potentially reproductive, coyotes. We recommend coyote removal efforts be directed in close proximity to the grazing allotments in need of depredation relief and as late in the winter season as practical. Based on current understandings, we believe management programs for coyotes in mountainous regions need not incorporate special biological considerations with regard to seasonal movements compared to other environmental situations.

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